

# HINDLIMB PROPORTIONS AND LOCOMOTION OF *EMUARIUS GIDJU* (PATTERSON & RICH, 1987) (AVES: CASUARIIDAE)

WALTER E. BOLES

Boles, W.E. 1997 06 30: Hindlimb proportions and locomotion of *Emuarius gidju* (Patterson & Rich, 1987) (Aves: Casuariidae). *Memoirs of the Queensland Museum* 41(2): 235-240. Brisbane. ISSN 0079-8835.

Using proximal and distal fragments, the length of the tarsometatarsus of *Emuarius gidju* is estimated and compared to that of other hindlimb elements. From these proportions and other hindlimb morphology, the inferred locomotory mode of *E. gidju* is compared with Recent casuariids. *Emuarius gidju* appears to have been more cursorially adapted than *Casuarius* and dwarf *Dromaius*, suggesting at least some open habitat in the Riversleigh palaeoenvironment. Using the relationship between weight and least circumference of the femur and tibiotarsus in Recent birds, the weight of *E. gidju* is suggested to have been 19-21kg. □ *Emuarius, Aves, hindlimb, locomotion.*

Walter E. Boles, Australian Museum, 6 College Street, Sydney NSW 2000, Australia; received 4 November 1996.

Emus, *Dromaius* (Dromaiinae), form a prominent element of Australia's avifauna. The closely related cassowaries, *Casuarius* (Casuariinae), are more restricted in distribution. These two groups occupy very different modern habitats, and locomotory adaptations correlated with these different habitats are obvious in the relative proportions of the lower limb bones. Because of the relationship between habitat and limb proportions, fossil emus and cassowaries are potentially good palaeoenvironmental indicators. Emus have a better fossil record (Patterson & Rich, 1987), than cassowaries (Vickers-Rich, 1991). Patterson & Rich (1987) described lower limb elements from the Miocene of central Australian as a small emu, *Dromaius gidju*. Boles (1991) erected *Emuarius* for this species and considered it closer to emus than cassowaries, but nearer their dichotomy than any other described taxon.

The type material of *Emuarius gidju* is part of the Kutjamarpu Local Fauna, recovered from the Leaf Locality (UCMP V-6213) on the E shore of Lake Ngapakaldi in the E Lake Eyre Sub-Basin, South Australia. Much *E. gidju* material occurs at Riversleigh NW Queensland. Archer et al. (1989, 1994) considered the Riversleigh palaeohabitat as rainforest, based on mammal remains.

This paper is to 1) estimate the lower limb proportions of *E. gidju*; 2) compare these to modern emus and cassowaries and, by implication, to their style of locomotion; 3) make an initial estimate of the weight of *E. gidju*; and 4) interpret the possible palaeohabitat at Riversleigh where *E. gidju* occurs.

## MATERIALS AND METHODS

Osteological terminology follows Baumel & Witmer (1993). Measurements were made with vernier calipers accurate to 0.05mm and rounded to the nearest 0.1mm. Institutional acronyms are AM (Australian Museum), QM (Queensland Museum) and SAM (South Australian Museum).

The type specimen of *E. gidju* (SAMP26779) is an associated distal tibiotarsal fragment, proximal tarsometatarsus including much most of the shaft, and complete set of pedal phalanges (Patterson & Rich, 1987) and numerous specimens of *Emuarius* are known from Riversleigh (Table 1).

To compare changes in relative proportions of the casuariid hindlimb, the following measures were calculated for the bone lengths of the 3 extant species of *Casuarius* and the 1 living and 2 recently extinct dwarf species of *Dromaius*:

$$TBT/FMR = \frac{\text{Tibiotarsus} \times 100}{\text{Femur}}$$

$$TMT/FMR = \frac{\text{Tarsometatarsus} \times 100}{\text{Femur}}$$

$$TBT/TMT = \frac{\text{Tibiotarsus} \times 100}{\text{Tarsometatarsus}}$$

Because the purpose was to find general, rather than detailed, directions of change, measurements were taken from the literature (Table 2) and rounded to the nearest mm. Means were used where available. The sample sizes were often small, sometimes comprising single individuals.

Predicted body weight of *Emuarius gidju* was calculated (Campbell & Marcus, 1991) from AM F78585 (near complete femur) and QMF16827

(distal tibiotarsal fragment). Tape was wrapped around the bones at their least circumferences, marked at the point of overlap, straightened and measured with calipers. These results were used in the equation  $\log_{10}(\text{weight})=a \cdot \log_{10}(\text{circumference})+b$ , where the values of  $a$  (slope) and  $b$  (intercept) were those determined by Campbell & Marcus (1991) for all birds for the respective elements (femur:  $a=0.411$ ,  $b=-0.065$ ; tibiotarsus:  $a=2.424$ ,  $b=0.076$ ).

## RESULTS

Increased cursoriality in these birds is associated with an increase in the lengths of the tibiotarsus and tarsometatarsus relative to that of the femur (Howell, 1944). Relative proportions of the hindlimb contributions of the long bones in *Casuarius*, *Dromaius* and *Emuarius* (Fig. 2) show that that of the tibiotarsus remains more or less consistent in all taxa; that of the femur decreases with increased cursoriality, whereas that of the tarsometatarsus increases. The relationship between these changes is consistent for Recent species:  $\text{TBT/FMR} = 0.45 [\text{TMT/FMR}] + 113$ ;  $r=0.84$ .

These changes appear independent of overall size when compared between genera, but within genera the smaller members have the greater TBT/TMT and smaller TMT/FMR. The TBT/FMR in *Casuarius* remains constant. It suggests from these figures that the smaller species in each genus are the least cursorial members.

The Kutjamarpu femur (AMF78585; Boles, 1991) of *E. gidju* is 194mm long, which, because of abrasion, is a few mm less than its original length, of about 198mm and very likely not 200mm. Complete tibiotarsi are unknown for *E. gidju* (Table 1). Nevertheless, it is possible to predict the size and relative proportions of this bone from other hind limb elements. Tarsometatarsi are represented by the holotypical proximal end and shaft, and several distal fragments. An estimate of the tarsometatarsal length was made by using the proximal end and shaft and a distal fragment. The proximal tarsometatarsal fragment is 276mm long; the longest edge of its shaft is straight and shows no evidence of flaring outward to trochlea metatarsi II. The distal piece is 64mm long; the small portion of shaft remaining is just proximal to the flaring of trochlea metatarsi II. Because there is little, if any, overlap between these two pieces, minimum length of the tarsometatarsus is 340mm (Fig. 3).

TABLE 1. Specimens that have been referred to *Emuarius gidju*. \*=specimens described by Boles (1991).

SITE	REG. NO.	ELEMENT
Lake Ngapakaldi	SAM P26779	Holotype: associated distal tibiotarsus, proximal tarsometatarsus, complete pes
	AMF78585*	Femur
Riversleigh		
System A or B White Hunter	QMF16827*	Tibiotarsus
System B Camel Sputum	QMF29720	Vertebrae
	QMF29721	Vertebrae
	QMF16828*	Femur
	QMF16829*	Femur
	AMF78586*	Tibiotarsus
	QMF29722	Tibiotarsus
	QMF29723	Tarsometatarsus
	QMF29724	Tarsometatarsus
	QMF29725	Tarsometatarsus
	QMF29726	Tarsometatarsus
Upper	QMF16830*	Rostrum
	QMF16831*	Scapulocoracoid
	QMF29728	Vertebrae
System ?B, Dirks Towers	QMF29729	Tarsometatarsus
System C Gag	QMF16832*	Femur
	AMF78587*	Tarsometatarsus

Using a tarsometatarsal length of 340mm and a femoral length of 198mm, gives a TMT/FMR of 172, greater than that of any Recent casuariid except *Dromaius novaehollandiae*. Using these values with the regression equation for the family (Fig. 4) gives a predicted TBT/FMR of 190, which corresponds to a tibiotarsal length of 376mm. These 3 values give a combined length of 916mm, virtually the same as the hindlimb of *Casuarius casuarius*, although the proportional contribution of each bone to this length is different (Fig. 2).

This figure must be used with caution. The fragments on which it is based represent different individuals from different localities. As such, there are several sources of potentially significant variation between components. Geographical variation may not have been of major importance; living *D. novaehollandiae* exhibits little differentiation across its range. There is much greater size variation across this species' chronological



FIG. 1. Leaf Locality femur of *Emuarius gidju* compared with femora of Recent casuariids, in cranial view. From left, *Casuarius Casuarius*, *C. bennettii*, *Emuarius gidju*, *Dromaius novaehollandiae* and *D. ater*.

range, with mainland fossils usually smaller than modern birds. Patterson & Rich (1987) suggested that it 'may have been at any one time in the Pleistocene both larger or smaller than at present'. Considerable intraspecific variation in living *D. novaehollandiae* is probably related to age and sex, as well as individual differences (Marchant & Higgins, 1990). For example, among 22 modern specimens, Patterson & Rich (1987) found a range in tarsometatarsal length of 332–422mm (mean 383mm; s.d. 18.0).

Miller (1963) described *Dromaius ocyopus* from the middle to late Pliocene Palankarina Local Fauna from Lake Palankarina, northern South Australia. This species was intermediate in size between *Emuarius gidju* and living *Dromaius novaehollandiae*. The tarsometatarsus of *D. ocyopus* is markedly shorter relative to its width than is that of *D. novaehollandiae*, but less so than in *Casuarius*. Vickers-Rich (1991) interpreted this as suggesting a less cursorial lifestyle for *D. ocyopus* than for *D. novaehollandiae*. Because Patterson & Rich (1987) did not give comparative figures for relative widths, it is difficult to quantitatively compare *E. gidju* with these species. Visually, *Emuarius* appears to be proportionally thinner for its length than is *D. ocyopus*, but not to the degree of *D. novaehollandiae*.

Patterson & Rich (1987) pointed out that, although, the foot of *E. gidju* is more like that of emus than cassowaries, it is more cassowary-like

than any known species of emu (illustrated in Patterson & Rich, 1987). In emus, phalanx unguis of digit III is longer than that of digit II, whereas in cassowaries it is reversed, with phalanx unguis of digit II extended into a long spike several times the length of phalanx unguis of digit III. *Emuarius* does not have phalanx unguis of digit II developed into a spike, but it is still longer than that of digit III.

Cassowaries have digits II and IV relatively long compared with digit III (ratios of II:III and IV:III, respectively, without phalanges unguales 0.82, 0.76). Both are substantially reduced in relative length in emus (ratios as above - 0.55, 0.63). Both digits II and IV of *Emuarius* are comparatively

longer than those in emus (digit IV to a lesser degree), but not to the extent seen in cassowaries (0.57, 0.68). Patterson & Rich (1987) suggested that the reduction of digit IV and particularly of digit II in *E. gidju*, compared with the highly cursorial *D. novaehollandiae*, appears to parallel similar reductions in other groups of terrestrial birds and mammals.

In comparison with the pedal phalanges of cassowaries, those of emus are dorsoplantarly compressed. *Emuarius* is somewhat intermediate, with its phalanges substantially more dorsoplantarly compressed than those of cassowaries, but less compressed than (but more similar to) the condition in emus.

Campbell & Marcus (1991) stated 'the least shaft circumference of either [femur or tibiotarsus] can be a reliable indicator of the weight of a fossil bird'. From their equation, and measurements of *E. gidju* bones, predicted weights of this species were 21kg based on the femur and 19kg based on the tibiotarsus. The least circumference of the tibiotarsus is almost always at or distal to the midpoint of the bone; in most birds it is in the distal third (Campbell & Marcus 1991). No tibiotarsal specimen of *E. gidju* is complete, although the length of that measured is about a third of the predicted length for this bone. It is possible that the least circumference occurs on the missing section of tibiotarsus, and the value given here would have to be adjusted. The predicted

TABLE 2. Measurements (mm) and measures of relative proportions of hindlimb bones of Recent emus and cassowaries and of *Emuarius gidju*. For calculation of predicted measurements of *E. gidju* and of measures of relative proportions, see text.

Species	FMR	TBT	TMT	Source	TBT/ FMR	TMT/ FMR	TBT/ TMT
<i>Dromaius novaehollandiae</i>	203	401	383	Patterson & Rich, 1987	198	189	105
<i>Dromaius baudinianus</i>	164	293	234	Morgan & Sutton, 1928	179	143	125
<i>Dromaius ater</i>	178	331	274	Morgan & Sutton, 1928	189	154	121
<i>C. casuarius unappendicularis</i>	236	388	306	Rich et al., 1988	164	130	127
<i>Casuarius casuarius</i>	232	384	300	Rich et al., 1988	166	129	128
<i>Casuarius bennetti</i>	221	365	229	Rich et al., 1988	165	104	159
<i>Emuarius gidju</i>	198	376	340	This paper	190	172	111

weights from the two bones are close enough to give an acceptable first estimate for *E. gidju*.

## DISCUSSION

Throughout the early Tertiary, much of Australia was covered in closed forest, and the climate was considerably more humid than at present (Frakes et al., 1987). The dominant vegetation type over much of the continent was rainforest. *Nothofagus*-dominated rainforest covered the Lachlan River valley during the late Eocene to late Oligocene-early Miocene (Martin, 1987). Even where closed forests were not present, gallery rainforest probably occurred along

watercourses. It was not until at least the middle Miocene (c. 15 mya) that drying of the climate began and open habitats started to appear on a large scale. There is no evidence of grasslands before the end of the late Miocene to Pliocene (Martin, this volume).

The graviportal locomotion of *Casuarius* is associated with movement through the dense vegetation of the Australo-Papuan rainforests. Increased cursoriality seems correlated with the appearance of more open habitat, in which sustained running could take place. (While able to run if required, cassowaries have

limited opportunities in such habitat to work up and sustain a reasonable degree of speed because sufficiently open areas are restricted.) Morphological correlates with cursoriality include proportional lengthening of the tibiotarsus and tarsometatarsus, and a reduction in the relative size of digit II. Conditions between the extremes of the states found in *Casuarius* and *Dromaius* are suggestive of levels of cursorial ability intermediate between theirs, although at what point along the scale cannot be determined. This, in turn, suggests the possibility that the amount of open habitat might be also somewhere between that available to cassowaries and emus.

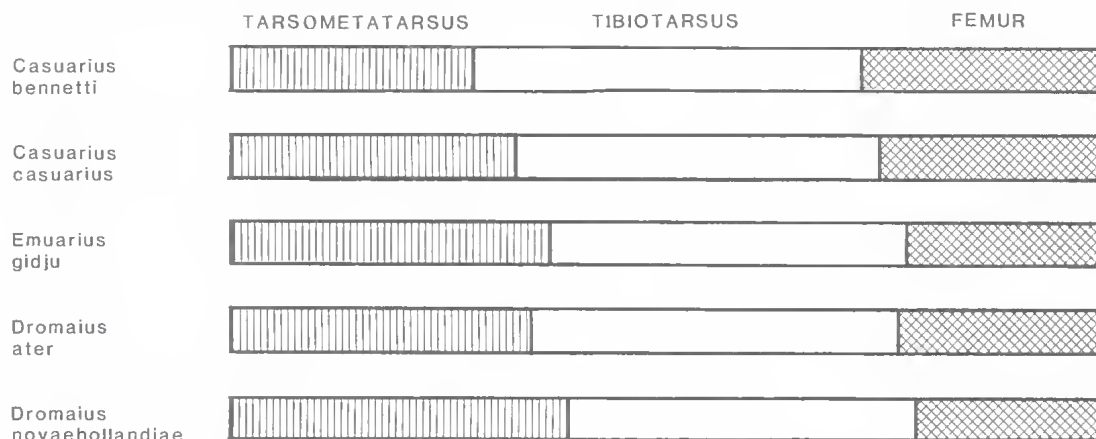


FIG. 2. Comparative proportions of bones in the hindlimbs of *Emuarius gidju*, two species of *Casuarius* and two species of *Dromaius*. Note that while the tibiotarsal proportion remains relatively constant, the proportion comprising the femur decreases as that of the tarsometatarsus increases.



FIG. 3. 'Combined' length of Leaf Locality proximal tarsometatarsus and Riversleigh distal tarsometatarsus compared with tarsometatarsi of Recent casuariids, in cranial view. From left, *Dromaius novaehollandiae*, *D. ater*, *Emuarius gidju*, *Casuarius casuarius* and *C. bennettii*.

*Casuarius* has been considered more primitive than *Dromaius* on the basis of distribution, habitat preferences and hindlimb. Schodde & Calaby (1972) and Schodde (1982) cited the cassowaries as elements of the Tumbunan avifauna, which represents the earliest lineages of extant Australo-Papuan birds. The emus were placed by Schodde (1982) in the autochthonous Eyrean fauna, which evolved in response to the opening of the Australian habitat. Boles (1991) considered *Emuarius* to be closer to the dichotomy of cassowaries and emus than any other known taxon, but too cursorially adapted and *Dromaius*-like to have been the common ancestor. It appears to mark in the Casuariidae a stage in the transition from a graviportal to a more cursorial locomotion. Although some characters of the hindlimb of *E. gidju* are more similar to either *Casuarius* or *Dromaius*, many are intermediate between living members of these genera (Boles, 1991). Boles (1991) drew attention to the fact that the lower limb bones were more similar to those of *Dromaius*, whereas the femur, whose proportions are more dependent on the bird's mass than its

locomotion (Prange et al., 1979), more closely resembled *Casuarius*.

There are alternative explanations that accommodate both the cursorial hindlimb proportions of *E. gidju* and the absence of open spaces. One possibility is that the ground cover of the rain forests was sufficiently open for cursorial animals to move rapidly without obstruction. For example, modern *Nothofagus* forests are frequently open below the canopy, without the dense understory of some other rain forest types (pers. obs.).

Neville Pledge (pers. comm.) suggested that a situation may have existed similar to that which occurred on Kangaroo Island when the dwarf emu *Dromaius baudinianus* was extant. Much of the island's vegetation was very thick and would have prevented rapid passage of a large animal such as the emu. Large mammals, however, forced runways through the vegetation, permitting them to move with comparable, albeit restricted, ease. The emus apparently took advantage of these runways for their own progress. Likewise, the large mammals known from Riversleigh may have opened similar pathways through the thick undergrowth, which could have been used by *E. gidju*. Nonetheless, *D. baudinianus* was also noted for being very fast and virtually uncapturable in open areas.

A small Miocene dromaiid from Alcoota, NT, is known from 2 phalanges and 3 unassociated trochleae (Patterson & Rich, 1987). These are of comparable size with *E. gidju*. There are slight differences in phalangeal morphology, and Patterson & Rich (1987) retained these specimens as *Dromaius* sp. indet. until more complete material is available. The Alcoota palaeohabitat has been interpreted as a lake, bordered by sedge or grassland, grading to woodland and gully forest (Murray & McGirian, 1992). This is a different environment than that interpreted for the older Riversleigh deposits. Even if the Alcoota dromaiid proves to be *E. gidju*, it would have limited relevance to reconstructing the Riversleigh habitats because of the age differences of the deposits. It would, however, suggest that *E. gidju* was preadapted for the more open Alcoota environment.

Models of this species' locomotory mode depend on extrapolations from living, non-congeneric relatives. These are speculative, and must be treated as such, while palaeoenvironmental reconstructions based on them require an even greater degree of caution.

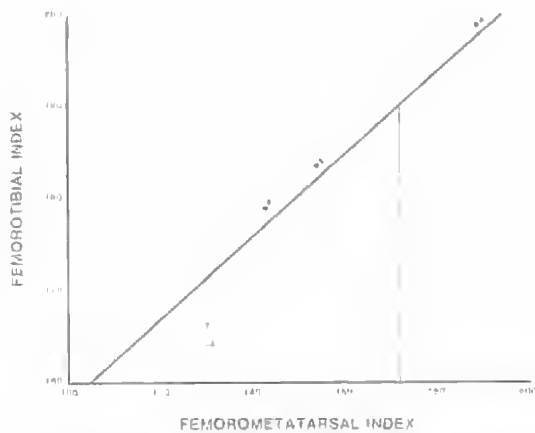


FIG. 4. Relationship of TMT/FMR and TBT/FMR of Recent species of *Casuarinus* (open circles) and *Dromaius* (closed circles). Species numbered as follows: 1. *Casuarinus bennetti*; 2. *C. casuarinus*; 3. *C. unappendiculatus*; 4. *D. baudinianus*; 5. *D. ater*; 6. *D. novaehollandiae*. Regression line is  $TBT/FMR = 0.45 [TMT/FMR] + 113$ ;  $r=0.84$ . The line vertical line represents the intersection with this line of the TMT/FMR (172) for *Emuarus gidju* as calculated in the text. Predicted TBT/FMR is 190.

#### ACKNOWLEDGEMENTS

In addition to acknowledgements in Boles (1991) I thank Neville Pledge for discussion on the Kangaroo Island habitat, Lynne Ho and Maurice Ortega for figures, and Anna Gillespie for information on *E. gidju*. The Riversleigh material was collected via an ARC Programme Grant to M. Archer; a grant from the Department of Arts, Sport, the Environment, Tourism and Territories to M. Archer, S. Hand and H. Godthelp; support from the University of New South Wales; a grant from the National Estate Programme Grants Scheme to M. Archer and A. Bartholomai; and grants in aid to the Riversleigh Research Project from Wang Australia Pty Ltd, ICI Australia and the Australian Geographic Society.

#### REFERENCES

- ARCHER, M., HAND, S.J. & GODTHELP, H. 1994. Riversleigh, 2nd ed. (Reed: Sydney).
- ARCHER, M., HAND, S., GODTHELP, H. & D. MEGIRIAN 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25: 29-65.
- BAUMEL, J.J. & L.M. WITMER. 1993. Osteologia. *Publications of the Nuttall Ornithological Club* 23: 45-132.
- BOLES, W.E. 1991. Revision of *Dromaius gidju* Patterson & Rich, 1987, with a reassessment of its generic position. *Natural History Museum of Los Angeles County Science Series* 36: 195-208.
- CAMPBELL, K.E. JR. & MARCUS, L. 1991. The relationship of hindlimb bone dimensions to body weight in birds. *Natural History Museum of Los Angeles County Science Series* 36: 395-412.
- FRAKES, L.A., MCGOWRAN, B. & BOWLER, J.M. 1987. Evolution of Australian environments. Pp. 1-16. In Dyne, G.R. & Walton, D.W. (eds), *Fauna of Australia* vol. 1A. General articles. (Australian Government Publishing Service: Canberra).
- HOWELL, A.B. 1944. *Speed in animals. Their specialization for running and leaping.* (University of Chicago Press: Chicago).
- MARCHANT, S. & HIGGINS, P.J. (coordinators). 1990. *Handbook of Australian, New Zealand and Antarctic birds, 1.* (Oxford University Press: Sydney).
- MARTIN, H.A. 1987. Cenzoic history of the vegetation and climate of the Lachlan River Region, New South Wales. *Proceedings of the Linnean Society of New South Wales* 19: 213-257.
- MILLER, A.H. 1963. Fossil ratite birds of the late Tertiary of South Australia. *Records of the South Australian Museum* 14: 413-420.
- MORGAN, A.M. & SUTTON, J. 1928. A critical description of some recently discovered bones of the extinct Kangaroo Island Emu (*Dromaius diemenianus*). *Emu* 28: 1-19.
- MURRAY, P. & MEGIRIAN, D. 1992. Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. *The Beagle* 9: 915-218.
- PATTERSON, C. & P.V. RICH. 1987. The fossil history of the emus. *Dromaius* (Aves: Dromaiinae). *Records of the South Australian Museum* 21: 85-117.
- PRANGE, H.D., ANDERSON, J.F. & RAHN, H. 1979. Scaling of skeletal mass to body mass in birds and mammals. *American Naturalist* 113: 103-122.
- SCHODDE, R. 1982. Origin, adaptation and evolution of birds in arid Australia. Pp. 191-224. In Barker, W.R. & Greenslade, P.J.M. (eds), *Evolution of the flora and fauna of arid Australia.* (Peacock Publications: Frewville).
- SCHODDE, R. & CALABY, J.H. 1972. The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. Pp. 257-300. In Walker, D. (ed.), *Bridge and barrier: the natural and cultural heritage of Torres Strait.* (Australian National University Press: Canberra).
- VICKERS-RICH, P. 1991. The Mesozoic and Tertiary history of birds on the Australian plate. Pp. 721-808. In Vickers-Rich, P.V., Monaghan, J.M., Baird, R.F. & Rich, T.H. (eds), *Vertebrate palaeontology of Australasia.* (Pioneer Design Studio: Melbourne).